

# THE LIFE-HISTORY OF A PENAEID PRAWN (*METAPENAEUS*) BREEDING IN A COASTAL LAKE (TUGGERAH, NEW SOUTH WALES).

By MURIEL C. MORRIS, M.Sc.,\* and ISOBEL BENNETT, Department of Zoology,  
University of Sydney.

(Plate xii and 96 Text-figures.)

[Read 26th September, 1951.]

## Synopsis.

This paper deals with the life-history of a species of Penaeid prawn (*Metapenaeus*, n. sp., Crustacea, Decapoda) and is based on a study of both living and preserved specimens. The species is unique in that the whole life-cycle from egg to breeding adult is spent in a shallow coastal lake (Tuggerah, New South Wales); in all other species whose life-histories are known, the maturing adults migrate from estuarine waters to the sea, the larvae returning to the estuaries.

Stages from egg, through nauplius, protozoa, mysis, post-mysis and post-larval to adult were obtained and the larval stages are described and figured hereunder. The life-history follows the same general lines as that described by Heldt (1938) for a Mediterranean Penaeid species.

## INTRODUCTION.

This study was part of the long-range programme of plankton and general marine investigations planned by the late Professor W. J. Dakin during his term of office as Professor of Zoology at Sydney University. This particular study was begun by him in 1945 and the field work was carried out by one of us under his direction during the years 1945-47. Two short notes indicating the general findings have already been published (Dakin, 1946, 1946a).

Professor Dakin had completed a large number of drawings and had made rough sketches and notes of all the stages in the early life-history before illness prevented his finishing the work. It was felt that this effort should not be lost, and, as one of us (I.B.) had been responsible for all the collecting, sorting and preserving of the stages, it was a relatively easy matter to complete the work.

## HISTORICAL.

The general story of the Penaeids, which are the Australian prawns of commerce, together with full details of the species concerned in the fishery, has already been told (Dakin, 1938, 1940, 1946).†

When prawn investigations were first begun in this Department, all the Penaeid species which could be obtained along the New South Wales coast were collected and sent, in 1937, to Mr. Martin D. Burkenroad, of the Bingham Oceanographic Foundation at Yale, who at that time was engaged in a systematic revision of Indo-Pacific littoral Penaeids. Burkenroad verified our identifications of *Penaeus esculentus* ('Tiger' prawn),

\* Formerly Linnean Macleay Fellow in Zoology.

† In the year 1947 a chance discovery by fishermen led to commercial fishing for prawns on a fairly large scale in open waters off the New South Wales coast. For the first time 'School' prawns, *Metapenaeus macleayi* (Haswell), with mature gonads, were found. This seemed to prove Professor Dakin's theory that this species, like *Penaeus plebejus*, also migrated from the estuaries to the open ocean to breed.

A brief survey of the American Penaeid fishery (which is of very much greater economic importance than the Australian fishery), together with details of the breeding migrations, is of interest in that it indicates a very similar story (Idyll, 1950).

Just as this paper was going to press we were shown several specimens of females of *M. macleayi* with spermatophores attached. These were taken in oceanic waters off the northern New South Wales coast in the month of February, 1951, by Mr. J. H. Wharton, Biologist, State Fisheries Department.

*P. plebejus* ('King' prawn) and *Metapenaeus macleayi* ('School' prawn), but in a letter dated 30/7/38, stated:

"Your two '*Metapenaeus monoceros*' from Lake Illawarra may be of the 'Dana' species, or possibly of *M. incisipes* Bate, or of my (MS.) *M. tweedii*, or of some other form. They are certainly not *M. monoceros*—since of the eight or ten species of the group (unpublished studies) this last is the one which does not range east of India. Determination of members of this group is difficult; it depends chiefly on details of the genitalia.

"When you deal with hairy prawns with numerous but minute lateral telson armature, you are on difficult ground. I am unable to say how many *Metapenaeus*, which usually pass under the name of *M. monoceros*, may occur in the region of Sydney, but I now have records of two species. One of these, the 'Dana' sp. n., must at some season be frequent in your commercial catch, since the sample, from Sydney market, consists entirely of it. As the specimens are large and adult, they may well have been taken at sea by the trawlers."

And later, on 18th January, 1940, Burkenroad wrote: "Your 'Greasy Backs' are the same as the 'Dana' *Metapenaeus* sp. n."

This prawn species which, because of the very thick covering of minute hairs on the carapace, was known locally to fishermen as the "Greasy Back", had always been regarded by Museum authorities and other workers in Australia as *Metapenaeus monoceros* Fabr.

We have been unable to contact Burkenroad since the end of World War II, and there is no mention of the genus *Metapenaeus* in the only published work on the 'Dana' collections we have seen (Burkenroad, 1940). In order to avoid possible duplication, we have decided to refer to the species simply as quoted above from Burkenroad's letter, "Dana" *Metapenaeus* sp. n.

After Professor Dakin had first obtained our so-called *Metapenaeus monoceros* from Lake Illawarra (see Dakin, 1938, p. 166), efforts were made over the years to procure further specimens of this species. We were successful in obtaining only a few specimens in the summer months of 1938–39 from Cook's River, Sydney. These were all sent to Burkenroad, who stated they were also the "same as my 'Dana' *Metapenaeus* sp. n.". On the outbreak of war in 1939, this work was discontinued, but in February, 1945, we discovered that these same prawns were forming the bulk of the commercial catch sent to the markets, and inquiry indicated that they were being caught in Tuggerah Lakes (three closely-connected lakes, Tuggerah, Budgewoi and Munmorah), 70 miles north of Sydney. Cooked prawns in which the gonads were fully mature were obtained from the Sydney Fish Markets. The prawns themselves were comparatively small, only 3½ to 4 inches in length.

It is characteristic of the shallow coastal lakes along the New South Wales coast to become silted up at the entrance, and, especially in dry periods, to remain closed sometimes for as long as two years. It had been hoped to make a series of observations on the various Penaeid species under these conditions, particularly in view of the known habit of the group, in other parts of the world, of migrating to open ocean waters to breed.

At this same time (early in 1945) it was learned that Tuggerah Lakes had been closed for a period of approximately two years, and that the 'King' and 'School' prawns, by the end of the second year (the summer season 1944–45) were scarce but very large. None, however, was observed with any gonads. But the 'Greasy Backs' which, in that particular season, were very numerous, forming the bulk of the catch, all had mature gonads. This information seemed to fit in very well with our theories regarding the three species concerned. By the time all these details were known, it was too late in the season to carry out any field work to obtain larval stages, but plans were made for an intensive effort for the next summer season (the months of November, December, 1945, and January–March, 1946).

Unfortunately heavy rains caused flooding in the lake backwaters during the autumn, and in May, 1945, the entrance to Tuggerah Lakes was cut through and the

lakes have not been completely land-locked since that date. This entirely altered the physical conditions within the lakes, but the work was carried out as planned.

Fishermen who tested the prawning grounds in the lakes stated that small prawns first began to appear in October, but these were well under regulation size ( $3\frac{1}{2}$  inches). By November, 1945, however, intensive fishing was being carried on with three species of prawns appearing in the catches—*P. plebejus*, *Metapenaeus macleayi*, and the so-called "Greasy Back". The two former were taken together, mainly in the largest lake, Tuggerah itself, and always at night. The "Greasy Backs" were generally caught alone in both Tuggerah and Budgewoi Lakes, and had a habit of shoaling during the day.

Many bulk catches were examined from different parts of the lakes and though a very careful search was made throughout the whole period of the investigation (1945-47) we were never successful in finding either *P. plebejus* or *M. macleayi* in the lakes with any signs of developing gonads.

From November to March, however, the "Greasy Back" females were very conspicuous in all catches because the gonads showed up as a dark green band along the dorsal surface of the abdomen (Plate xii, fig. 2). Random samples of many hundred specimens were taken, and the individuals sexed and measured. It was found that the females were larger than the males—the largest female actually measured by us being 5 inches, though the greatest number averaged between  $3\frac{1}{2}$  and 4 inches. We found only one male as long as 4 inches, the greater proportion being about 3 inches. The females in all samples counted formed more than 50% of the total catch, but it was felt that this was probably due to the size of the mesh of net used by the fishermen.

Close examination of specimens led us to suspect that, in common with many other marine animals, spawning took place at time of full moon. Our catches later substantiated this.

#### COLLECTION OF MATERIAL.

Since, to our knowledge, there had been no previous plankton collections in Tuggerah Lakes, a great number of exploratory hauls had to be made, and these were carried out on all three lakes. Nets of varying degrees of coarseness were used, from the finest mesh bolting silk to nets of coarse stramine. Since overseas work had indicated (Pearson, 1939) that the eggs were probably demersal, various methods, such as the attaching of heavy iron sledges to the nets, had to be devised for taking hauls just above the bottom layer of mud. This was extremely difficult since the floor of the lakes, which was only about 8 feet deep in the deeper parts, was very uneven. On more than one occasion in heavy southerly weather, the hauls had to be abandoned and a fresh start made after the net had become clogged with mud from the bottom.

Another difficulty, accentuated by the opening of the lakes to the sea, was the seasonal influx of Coelenterates. Finally two types of cones which had the same diameter as the net and which fitted over the mouth of the net, were used. One was made of flat galvanized sheeting with small holes punched all over it, and the other of small gauge wire netting. The guy ropes of the net were threaded through a hole in the peak of the cone, the base of which was firmly laced to the ring of the net. The current set up by these cones as the nets were pulled through the water served, to a certain extent, to force the jelly fish out of the course of the net, and the holes and wire mesh permitted the net to catch smaller organisms. The method was quite successful when dealing with the large medusa, *Catostylus mosaicus*, but when the Ctenophores came into the lakes, all our efforts were practically useless. The surface waters were almost solid Ctenophora, which were so soft that the cones merely broke them and the nets became coated with a thick gelatinous slime.

A large number of hauls using the different nets were taken at close intervals throughout the summer seasons of 1945-46 and 1946-47. Throughout the winter months of 1946 regular monthly hauls were made so that some idea would be gained of the general plankton constituents throughout the whole year.

Since we are able to state with certainty that no other Penaeid prawn taken in the lakes during this time had even immature gonads, and since the bulk of our catches were taken in Budgewoi Lake, at least eight miles from the entrance, where



there is no tidal flow, we have no hesitation in regarding the eggs and nauplii as those of the breeding *Metapenaeus*.

We were successful in obtaining eggs during February and March only, but Protozoa and Mysis stages were found in all months from November to March inclusive. We cannot be certain of the full number of nauplii but the most important stages in development were verified with living material. No aquarium facilities of any kind were available to us, but by means of a temporary laboratory set up in a tent on the lake shore we were able to watch the egg developing through 2, 4, 8, and 16 cell stages, and finally photographed several in which the nauplius could be seen actively moving round within the egg membrane. The newly hatched nauplius was also photographed (Plate xii, fig. 3). What we considered to be the last nauplius (*Metanauplius*) stage moulted into Protozoa I. We also observed the moulting of Protozoa I into Protozoa II, Protozoa II into Protozoa III, and Protozoa III into Mysis I.\* It was only after very considerable difficulty and a week's concentrated effort that Mysis III stages were obtained. It is interesting to note here that we had chosen a particular week in February to make these catches, ten to eleven days after the full moon. In that week practically no stages other than late Mysis were found in any of the catches. This substantiated the assumption that spawning takes place at the time of full moon, as the time taken for an egg to develop to a late Mysis stage is about ten days. No Mysis were found in the surface hauls and it was only when the nets were weighted and hauled just above the bottom that we were successful in finding them. Heldt (1938) found that this was also the case with her Mediterranean Penaeid species: "Dans les pêches de plancton la quatrième mysis et la première post-mysis sont très rares."

We were able to keep most of the late Mysis alive until the first post-Mysis stage, but without aquarium facilities were unable to go further. From the above, however, we were able to place with certainty all our planktonic material as belonging to the one species. A very long series of post-larval stages from  $\frac{1}{4}$  inch in length and leading to the young adult, finally left us in no doubt about the identity of the species of which they were the larval stages.

#### LARVAL AND POST-LARVAL STAGES.

A series of 16 larval stages was taken in the plankton hauls. They consisted of four Nauplius stages, three Protozoa stages, three Mysis stages and six post-Mysis stages. In addition several post-larval stages were taken, four of which have been described.

The Nauplius stages taken did not constitute a complete series, and it would seem that the full series, as obtained by Heldt, numbers eight—the possible missing stages being two, three, four and six. The three Protozoa, of course, constitute the full number of Protozoa stages, while three distinct Mysis stages have been obtained. Heldt (1938) records four Mysis stages for *Penaeus trisulcatus*, while the American workers record only two for their species.

There is quite a big gap between the first post-Mysis, which was obtained by direct moulting, and the next stage taken in the plankton hauls (5.073 mm.). From the 5.073 mm. stage onwards a series of ten stages (to 23.572 mm. stage) were taken. The first five of these are probably post-Mysis stages, while the other five are post-larval. The distinction between post-Mysis and post-larval stages has been made on the purely morphological basis that the first stage bearing biramous pleopods would be the first post-larval stage. The important difference between post-Mysis and post-larval stages is that propulsion is thoracic in post-Mysis and abdominal in post-larval. The loss of feathered exopodites from the pereopods (first post-Mysis stage) would mean a loss of effective thoracic propulsion. However, the fact that the pleopods are still ill-developed at this stage means that abdominal propulsion would be equally ineffective. In fact, abdominal propulsion would not be effective until the appearance of biramous pleopods (7.835 mm. stage), and for this reason it is felt that this stage should be

\* We have followed Heldt (1938) rather than Gurney (1927 and 1942) in the terminology used for these stages.



considered as the first post-larval stage. It is realized, of course, that ever since the appearance of a well-developed tail-fan at the moult to first Mysis, flexing of the abdomen has no doubt constituted quite an effective means of propulsion. Madame Heldt (1938) referred to the role of abdominal flexion in propulsion, but without the observation of live specimens, which was not possible in this study, it would not be possible to say just how effective a means of propulsion this would be in *Metapenaeus*. Heldt (1938) made this division into post-Mysis and post-larval at an earlier stage—she named the first post-larval as the stage preceding the one where biramous pleopods appeared.

#### NAUPLIUS STAGES.

*First Nauplius* (Text-fig. 1).—Several very early stages in the development of the nauplius, all still enclosed in the egg membrane (Plate xii, fig. 3), were taken. They later emerged as the first Nauplius larva.

The first Nauplius measures 0.23 mm. from the front end to the end of the body (not including the spines). The body is somewhat pyriform in shape when viewed from the dorsal or ventral aspect, but when viewed from a lateral aspect it has a ventral flexure. At this stage the body shows no signs of segmentation.

A pair (1 + 1) of spines extend out from the posterior margin of the body.

A Nauplius eye lies on the median ventral surface of the body close to the anterior border. This eye persists through to the Protozoa stages and probably into the Mysis stages.

The three pairs of appendages present at this stage, first and second antennae and mandibles, are large unsegmented club-shaped structures with a purely natatory function.

The first antenna (Text-fig. 1) is a uniramous appendage bearing three terminal setae and also three on the inner side and one on the outer side.

The second antenna (Text-fig. 1) is a biramous appendage bearing three terminal setae on the endopodite and one short spine and two terminal setae and three lateral setae on the exopodite.

The mandible (Text-fig. 1) bears no cutting surface at this stage, but consists of a biramous appendage. The exopodite bears three terminal setae, whilst the slightly longer endopodite bears two terminal setae and one on the inner side.

*Fifth Nauplius* (Text-fig. 2).—The next Nauplius stage which was taken in the catches corresponds to Heldt's fifth Nauplius for *Penaeus trisulcatus*. The only differences between Heldt's fourth and fifth nauplius stages are an increase in size; the presence of seven segments in the exopodite of the second antenna of the Nauplius four and eight in Nauplius five; and the growth of the terminal spine on the endopodite of the second antenna of the fourth Nauplius into a long hair in the fifth Nauplius.

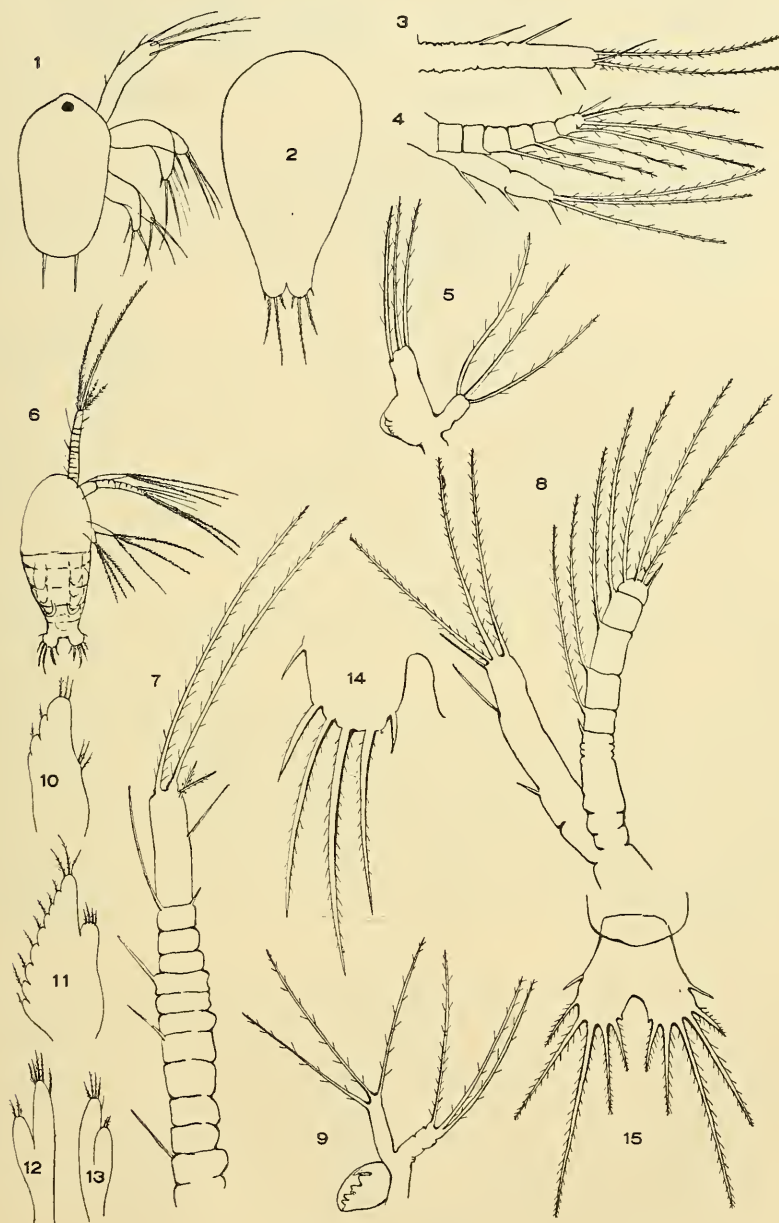
As the exopodite of the second antenna of this stage of *Metapenaeus* consists of seven and not eight segments, it would seem that it is a fourth Nauplius stage. However, the presence of three well-developed hairs and a spine on the endopodite of the second antenna identify it as a fifth Nauplius. Actually, Heldt gives the presence of three plumose hairs and a spine on the endopodite of the second antenna as one of the characteristics of the sixth Nauplius in *Penaeus trisulcatus*. However, the fact that the telson bears four pairs (4 + 4) and not six pairs (6 + 6) of spines at this stage of *Metapenaeus*, definitely classifies it as a fifth Nauplius.

The length of the body is now 0.27 mm.–0.29 mm., and the following significant changes have taken place since the first Nauplius stage.

The posterior border of the body is now quite deeply indented to form a definite furca bearing four pairs of spines. The first antenna (Text-fig. 3) is now segmented and the beginnings of a large number of segments are obvious at the base. It bears two long plumose hairs and a short spine at the end; two small hairs well towards the distal end on the outer side; two longer hairs on the inner margin—one in the middle of the distal segment, and one further down.

The exopodite of the second antenna (Text-fig. 4) now consists of seven segments—the division between the last two segments still being ill-defined. The most distal, or seventh, segment bears two long plumose hairs and a small spine at its extremity, while

the 3rd, 4th, 5th and 6th segments each bear a large plumose hair on their inner distal margins. A small spine is present on the inner distal margin of the second segment. The endopodite, which is still unsegmented, bears three long hairs and a spine at its



Text-figures 1-15.

1, First Nauplius,  $\times 92$ .

2-5, Fifth Nauplius. 2,  $\times 120$ ; 3, First antenna,  $\times 131$ ; 4, Second antenna,  $\times 66$ ; 5, Mandible,  $\times 164$ .

6-14, Seventh Nauplius. 6  $\times 34$ ; 7, First antenna,  $\times 170$ ; 8, Second antenna,  $\times 171$ ; 9, Mandible,  $\times 284$ ; 10, First maxilla; 11, Second maxilla; 12, First maxillipede; 13, Second maxillipede; 14, Furca,  $\times 462$ .

15, Eighth Nauplius, Furca.

distal end; a shorter hair two-thirds of the way down and one one-third of the way down on the inner margin.

There is now a very definite swelling at the base of the endopodite of the mandible (Text-fig. 5) which will eventually give rise to the cutting surface of the future mandible. The outlines of teeth can already be seen through the chitin on the inner side of this swelling. The exopodite and endopodite still bear the same number of hairs as at the first naupliar stage.

The maxillae and first and second maxillipedes are now visible under the cuticle on the ventral side.

*Seventh Nauplius* (Text-fig. 6).—The next stage in the series which was taken corresponds to Heldt's stage seven for *Penaeus trisulcatus*. The presence of six pairs (6 + 6) of spines on the furca marks it as either a sixth or seventh Nauplius stage, but the facts that the posterior border of the carapace is beginning to appear, and that the maxillae and first and second maxillipedes are now free, identify it as a typical stage seven.

The body now measures 0.671 mm.

The number of segments in the first antenna (Text-fig. 7) has increased, an additional small spine has developed on the distal outer corner of the most distal segment, and an additional two have appeared on the inner side of the appendage.

Signs of further segmentation of the exopodite of the second antenna (Text-fig. 8) are evident; a third hair has appeared, while the small spine, which was present at the fifth Nauplius stage, has now developed into a small hair. The most distal segment of the exopodite thus bears the full complement of four hairs—or what will be four hairs—found in the Protozoa stages. The endopodite remains unchanged.

The swelling on the base of the mandible (Text-fig. 9) has increased in size, and the cutting surface is now clearly visible under the cuticle.

*Eighth Nauplius*.—One later Nauplius stage, with seven pairs (7 + 7) of the spines on the furca, was taken. Only one specimen was available for study and only the telson was drawn.

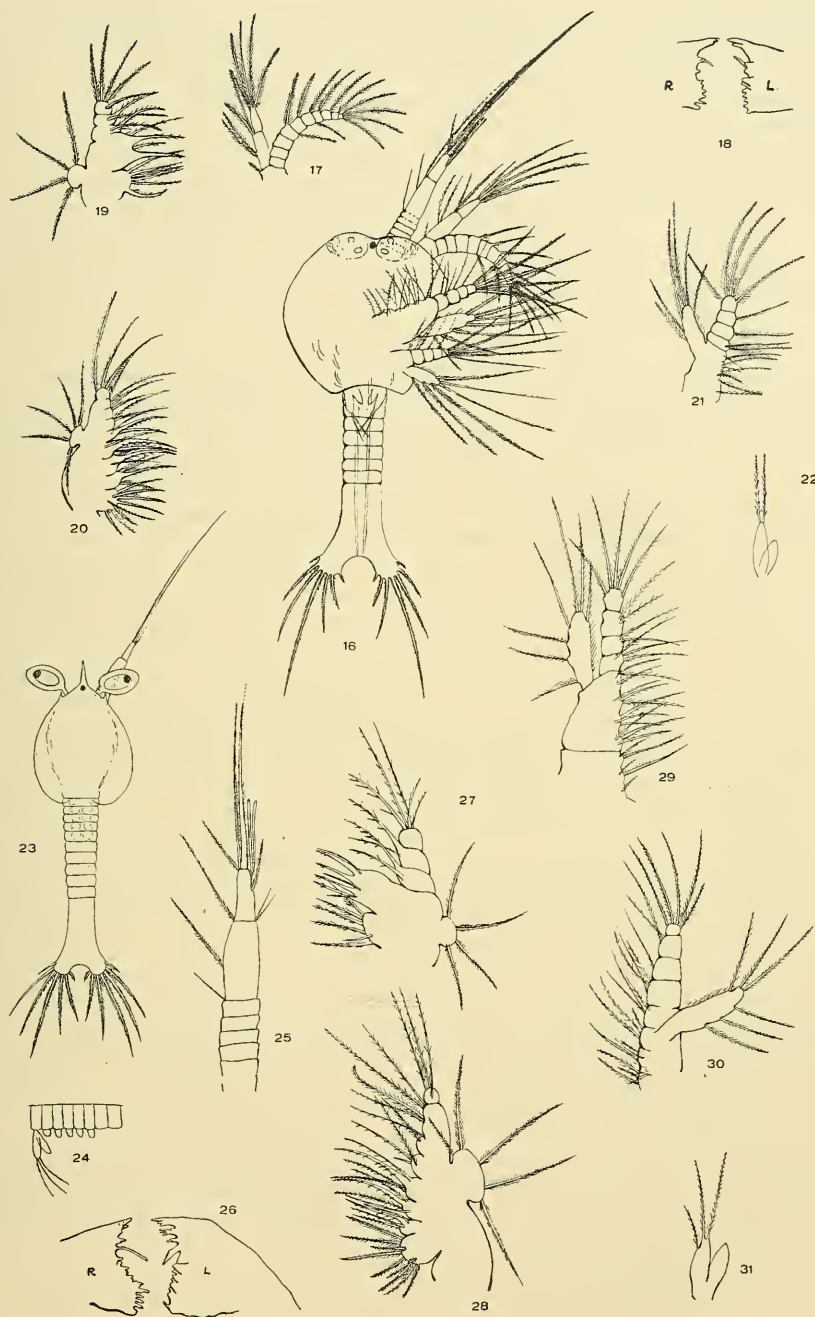
As the telson (Text-fig. 15) bears seven pairs of spines, it undoubtedly is a very late Nauplius stage. The degree of development of the maxillae and first and second maxillipedes at our seventh Nauplius makes it highly unlikely that there would be more than one Nauplius stage between Nauplius seven and the first Protozoa stage. It seems evident, then, that the telson figured belongs to the eighth Nauplius stage. Only two specimens of very late nauplii were found by us in the plankton catches. One, of which the telson is figured, was preserved, and the other which, so far as we could judge from low-power magnification of a living specimen in the field, was identical with it, moulted to the first Protozoa.

#### PROTOZOA STAGES.

The last Nauplius stage is followed by the Protozoa stages. As Heldt (1938) has dealt very fully with the change in habits that accompany the change from the last Nauplius to the first Protozoa, it is not intended to cover this ground again. However, two factors which influence the future development of certain appendages of the Protozoa stages should be mentioned. These are, firstly that the larva now feeds and there is a great development of the maxillae and the cutting surface of the mandible; secondly, that certain of the thoracic appendages, the maxillipedes, now aid the first and second antennae in propulsion. Up till the end of the sixth Nauplius stage the maxillae and first and second maxillipedes are not free. By the end of the seventh Nauplius stage they are free but still poorly developed. However, during the Protozoa stages they increase greatly in size, acquire quite extensive feathered surfaces and are thus able to aid the first and second antennae in propulsion.

*First Protozoa* (Text-fig. 16).—The larva now measures from 0.781 to 0.872 mm. in length. All the larval stages show quite a considerable variation in length. (All lengths are from the base of the rostrum to the end of the telson—not including the rostrum or telson spines.)





Text-figures 16-31.

16-22, First Protozoa. 16,  $\times 54$ ; 17, Second antenna,  $\times 68$ ; 18, Mandible,  $\times 67$ ; 19, First maxilla,  $\times 130$ ; 20, Second maxilla,  $\times 123$ ; 21, Second maxillipede,  $\times 91$ ; 22, Third maxillipede,  $\times 148$ .

23-31, Second Protozoa. 23,  $\times 31$ ; 24, Lateral aspect of abdomen; 25, First antenna,  $\times 115$ ; 26, Mandible,  $\times 167$ ; 27, First maxilla,  $\times 160$ ; 28, Second maxilla,  $\times 164$ ; 29, First maxillipede,  $\times 126$ ; 30, Second maxillipede,  $\times 130$ ; 31, Third maxillipede,  $\times 135$ .

The shape of the body has changed considerably. It now consists of an enlarged oval anterior section, making up a little less than one-half the total body-length, and a long cylindrical hind portion, the abdomen. The abdomen, which is still unsegmented, ends in the now widely-forked telson, which still bears seven pairs (7 + 7) of spines. The fourth, or middle pair of spines is the largest, and remains so right up to the post-larval stages.

The Nauplius eye is still present. The paired adult eyes are visible as two opaque masses situated just beneath the carapace at the anterior margin of the body.

The first antenna (Text-fig. 16) consists of a basal five-segmented portion and two long distal segments. There are two large and one small terminal setae; two near the end on the outer side; and one on the inner side at the junction of the two large segments; one half-way down the second segment; and one on the most distal of the five basal segments.

The exopodite of the second antenna (Text-fig. 17) now consists of ten segments, while the endopodite has two segments. The last or most distal exopodite segment now bears four long terminal hairs—the small hair of the Nauplius seven stage having developed into a long plumose hair. The 4th, 5th, 6th, 7th, 8th and 9th segments each bear a hair on their internal borders, while the 4th and 6th segments each bear an external hair. The endopodite now bears five terminal hairs; and on the inner margin two at the junction of the two segments and two half-way down the first segment.

The mandible (Text-fig. 18) has now lost its biramous appearance, while the cutting surface, consisting of two distinct regions, is well developed. The right and left mandibles are quite similar at this stage, each having a long, pointed tooth and a short thick-set tooth separating the lower molar region of the mandible from the upper cutting region.

The first maxilla (Text-fig. 19) is a biramous appendage with a three-segmented endopodite and an unsegmented button-like exopodite. The two protopodite segments form two quite well-defined endites on their inner surface. The most proximal, or first, endopodite segment bears two hairs, the second two, while the terminal segment carries five. The exopodite carries four long plumose hairs, while the proximal endite carries six and the distal endite four rather short hairs.

The second maxilla (Text-fig. 20) is also a biramous appendage, the endopodite being five-segmented, while the exopodite again forms a button-like unsegmented structure. The first or most proximal endopodite segment carries three setae, the second two, the third two, the fourth two and the fifth three setae. The exopodite carries five long plumose hairs. The protopodite forms four endites on its inner surface carrying eight, four, four and three setae, numbering from the most proximal endite.

The first maxillipede (Text-fig. 16) consists of a four-segmented endopodite and an unsegmented blade-like exopodite. The endopodite carries three setae on the first segment, one on the second, one on the third, and five terminal setae. The exopodite carries two terminal setae and also one internal and four external. The protopodite carries a large number of hairs on its inner surface.

The second maxillipede (Text-fig. 21) closely resembles the first maxillipede at this stage, except that it is smaller. The endopodite is four-segmented, while the exopodite is once again an unsegmented blade-like structure bearing two terminal setae and also one internal and three external setae. The endopodite carries two setae on the first segment, one on the second, one on the third, and five terminal setae. Once again, the protopodite is thickly beset with hairs on its inner surface.

Both Heldt and Pearson found for their respective species of *Penaeus* that the third maxillipede was not present in Protozoa I, but in our species it has definitely made its appearance and is an unsegmented biramous appendage at this stage (Text-fig. 22). It carries two terminal setae on the exopodite.

Behind the third maxillipede, there are five distinct thoracic segments already formed, which, in the second Protozoa stage, will carry the buds of the pereopods.

*Second Protozoa* (Text-fig. 23).—The larva now measures from 1.0 mm. to 1.36 mm. in length.

The body still consists of the large anterior portion covered by the carapace, and a long cylindrical posterior portion. The carapace, which is lengthening rapidly and is now pear-shaped, still reaches only to the end of the ninth (third maxillipede) body segment. It is becoming more deeply indented posteriorly.

Anteriorly, the carapace now bears a rostrum and two supra-orbital spines, one on each side of the rostrum. The eyes at this stage are large and stalked and project well beyond the anterior corners of the carapace. The Nauplius eye still persists.

The six abdominal segments are now clearly visible, although the sixth is still not separated from the telson. The seven pairs of spines on the telson have increased considerably in size.

Apart from the acquisition of one seta half-way down on the outer side and a pair of hairs on the outer distal corner of the large second segment, the first antenna has undergone no change (Text-fig. 25). The second antenna has undergone no change at all.

The cutting surfaces of the mandibles (Text-fig. 26) display a definite dissimilarity between the right and left—the greater change having taken place in the left mandible.

The first maxilla (Text-fig. 27) carries an additional two to three setae on the distal endite, while the first or proximal endite and the fourth endite of the protopodite of the second maxilla (Text-fig. 28) each bear an additional seta.

The first maxillipede (Text-fig. 29) bears an additional seta on the inner surface of the second and third endopodite segments and a few extra setae on the proximal protopodite segment.

The second maxillipede (Text-fig. 30) which shows indications of a fifth endopodite segment, the first being very indistinctly divided from the protopodites, bears an extra seta on all the endopodite segments except the third.

The exopodites of the third maxillipede (Text-fig. 31) now bear three setae, two terminal and one on the outer edge.

Behind the third maxillipede the five thoracic segments, formed in the first Protozoa stage, now carry the buds of five pairs of peraeopods (Text-fig. 24).

*Third Protozoa* (Text-fig. 32).—The larva now measures from 1.53 mm. to 1.73 mm. in length, the greatest increase having taken place in the hind thoracic and abdominal regions.

The carapace, which still reaches only to the end of the ninth body segment, is now quite deeply indented at the posterior end. The supra-orbital spines, which are already decreasing in size, are now situated quite close together at the base of the rostrum.

The Nauplius eye persists.

The sixth abdominal segment, which is now completely separate from the telson, is by far the longest of the abdominal segments. The third, fourth and fifth abdominal segments each bear a median dorsal spine on their posterior borders; the fifth carries an additional dorso-lateral spine on each side. The sixth abdominal segment carries a minute pair of dorso-lateral and also a pair of ventro-lateral spines (Text-fig. 33). There are still no signs of abdominal pleopods.

The uropods are now completely free—the exopodite bearing six and the endopodite three setae. The telson still bears seven pairs of spines.

The first antenna (Text-fig. 34) now consists of four segments instead of the seven of the previous stage. This tendency towards a loss of flexibility of the first antenna is very important as it serves as a pointer to the fact that in the Mysis stages the first antennae will no longer be responsible for propulsion. The arrangement of setae has undergone no change since the previous stage.

The second antenna remains unchanged.

The dissimilarity between the right and left mandibles (Text-fig. 35) is now more evident. The right mandible bears two dentated spines between the molar and cutting regions, while on the left mandible, this intermediate region which was showing signs of forming spines in the previous stage, now bears seven spines, three of which are



dentated. The molar regions in both right and left mandibles have increased considerably in size.

Apart from the fact that the distal endite of the first maxilla (Text-fig. 36) now bears nine setae, the proximal endite eight, and the protopodite of the second maxilla (Text-fig. 37) now bears more hairs, the first and second maxillae have undergone no change since the previous stage.



Text-figures 32-54.

32-40, Third Protozoaea. 32,  $\times 24$ ; 33, Lateral aspect of abdomen; 34, First antenna; 35, Mandible,  $\times 82$ ; 36, First maxilla,  $\times 86$ ; 37, Second maxilla,  $\times 86$ ; 38, First maxillipede,  $\times 65$ ; 39, Second maxillipede,  $\times 54$ ; 40, Third maxillipede,  $\times 59$ .

41-54, First Mysis. 41, Lateral aspect of abdomen; 42, Ventro-lateral aspect of 6th abdominal segment; 43, Telson and uropods; 44, First antenna,  $\times 88$ ; 45, Lateral aspect of basal segment of first antenna; 46, Second antenna,  $\times 54$ ; 47, Mandible,  $\times 103$ ; 48, First maxilla,  $\times 83$ ; 49, Second maxilla,  $\times 103$ ; 50, First maxillipede,  $\times 62$ ; 51, Second maxillipede,  $\times 49$ ; 52, Third maxillipede,  $\times 65$ ; 53, First peraeopod,  $\times 51$ ; 54, Fourth peraeopod,  $\times 76$ .

The first maxillipede (Text-fig. 38) bears two extra setae on the exopodite—one on the outer border and one on the inner border, and there are one or two additional hairs at the base of the proximal protopodite segment.

The exopodite of the second maxillipede (Text-fig. 39) bears an additional seta on the outer border and there is also one on the outer edge of the endopodite.

The endopodite of the third maxillipede (Text-fig. 40) now bears two terminal setae, while the exopodite still bears three setae.

The five thoracic segments behind the third maxillipede now bear quite well-developed biramous appendages which still show no signs of segmentation or setation (Text-fig. 32).

#### MYSIS STAGES.

A. First Mysis (Text-figs. 41–54).

B. Second Mysis (Text-figs. 55–57).

C. Third Mysis (early stages, Text-figs. 58–62; late stages, Text-figs. 63–67).

With the moult from the third Protozoa to first Mysis stage, the larva undergoes several quite radical changes.

Undoubtedly the most important development, and one which changes the whole appearance of the larva, is the growth of the peraeopods.

At the end of the third Protozoa stage they are biramous, unsegmented buds, but by the first Mysis stage they are quite distinct biramous appendages showing signs of segmentation, and bearing several setae. Up till the end of the third Protozoa stage, the antennae and maxillipedes are responsible for the propulsion of the larva through the water. However, at the moult to the first Mysis stage, the first antennae lose their feathery and flexible appearance, and propulsion is taken over by the peraeopods, aided to a small degree by the rapid jerking of the abdomen and tail fan.

#### A. *First Mysis* (Text-figs. 41–54).

The larva now measures 2.07 mm. in length.

The carapace reaches to the end of the fourteenth body segment (i.e., to the end of the fifth peraeopod segment). The supra-orbital spines have practically disappeared.

The third, fourth and fifth abdominal segments (Text-fig. 41) no longer bear dorsal spines and the fifth segment has also lost its dorso-lateral spines. The sixth abdominal segment now bears a median dorsal spine; one pair of ventro-lateral spines and a well-developed ventral hook (Text-fig. 42).

The telson and uropods (Text-fig. 43) now form a well-developed swimming tail-fan, and the prominent indentation of the posterior border of the telson, which was so characteristic of the Protozoa stages, has completely gone. It is replaced by a very small indentation, the two lobes diverging only slightly. Each lobe still bears seven pairs (7 + 7) of spines, the outer two pairs now being placed further up the sides of the telson.

The exopodites of the uropods now bear a spine on the external border near the extremity in addition to eleven feathered setae along the internal border and tip. The endopodites bear ten setae.

The first antenna (Text-fig. 44–45) still consists of four segments, but now bears an internal unsegmented branch attached to the extremity of the third segment. This internal branch, which is about one-third of the length of the outer or fourth segment, bears two terminal setae. At the base of the basal segment, on the outer side, is a swelling with a squared distal corner. This swelling will eventually lodge the statocyst, while the squaring of the corner will give rise to the stylocerite. There are two feathered setae on top of the swelling. The basal segment also bears a well-developed spine on the ventral face towards the inner border.

The second antenna (Text-fig. 46) has undergone quite a radical change. The exopodite has lost all signs of segmentation, and now consists of a plate-like structure with eleven hairs along its borders—six internal, three terminal, and two external. The endopodite remains unsegmented and only bears five setae—two terminal and three on the internal border.

The mandibles (Text-fig. 47) which have undergone very little change since the previous stage and still show a very marked dissimilarity, now bear a small bud which will eventually give rise to the mandibular palp.

Apart from the possible loss of one seta from the proximal endite, the first maxilla (Text-fig. 48) has undergone no change.

The exopodite of the second maxilla (Text-fig. 49) has increased greatly in size and is now beginning to take on the shape of the scaphognathite which it will eventually form. It bears nine setae along its border, whilst the number of setae on the internal borders of the protopodite has also increased.

The first maxillipede (Text-fig. 50) has undergone little change except that the number of setae on the exopodite has decreased to seven again, while the number on the protopodite segments has increased.

Much the same type of development has taken place in the second maxillipede (Text-fig. 51). The number of setae on the exopodite has decreased to five, while the number on the protopodite segments has increased. Three of the endopodite segments now bear a seta on the outer edge.

The third maxillipede (Text-fig. 52) which was rudimentary at the last Protozoa stage, has undergone a marked development. The endopodite is five-segmented and carries a number of hairs on its internal and external borders and at the extremity, while the exopodite, which is not segmented, bears six hairs at its extremity.

It is in the pereopods (Text-figs. 53 and 54) that the most important change has taken place. In the third Protozoa they were rudimentary, biramous buds, but they now consist of a large unsegmented exopodite with eight terminal hairs, and a small unsegmented endopodite. The endopodite, which bears three to four hairs at the end, shows signs in the first three pairs, of bifurcation. This will eventually lead to the formation of the typical chelate appendages seen in the adult.

Slight swellings on the ventral surface of the abdominal segments (Text-fig. 41) indicate the future position of the five pairs of pleopods.

#### B. *Second Mysis* (Text-figs. 55-57).

The second Mysis measures from 2.14 mm. to 2.26 mm. in length.

The supra-orbital spines have disappeared from the carapace but the abdominal spines remain unchanged.

The slit between the two lobes of the telson is becoming smaller, while the space between the first and second and second and third spines is increasing (Text-fig. 56).

The exopodite of the uropods now bears twelve setae along the internal border and at the tip in addition to the spine on the external border. The endopodite still bears ten setae (Text-fig. 56).

The stylocerite on the basal segment of the first antenna (Text-fig. 57) is becoming more evident, while the ventral spine is still very obvious. The number of setae on the various segments has increased, while the internal branch has increased quite considerably in size and now makes up more than one-third of the length of the fourth or external antennular segment.

A spine has appeared on the external border of the exopodite of the second antenna a quarter of its length from the extremity. The endopodite is still one-half of the length of the exopodite.

The only change which has taken place in the mandible is an increase in relative size of the palp.

The first maxilla has undergone no change, except that, throughout all the Mysis stages, the endopodite is gradually decreasing in size.

The scaphognathite of the second maxilla has increased in size and now carries twelve hairs along its borders.

The first, second and third maxillipedes have undergone no change.

The endopodites of the pereopods have increased considerably in length and show signs of segmentation into five segments.

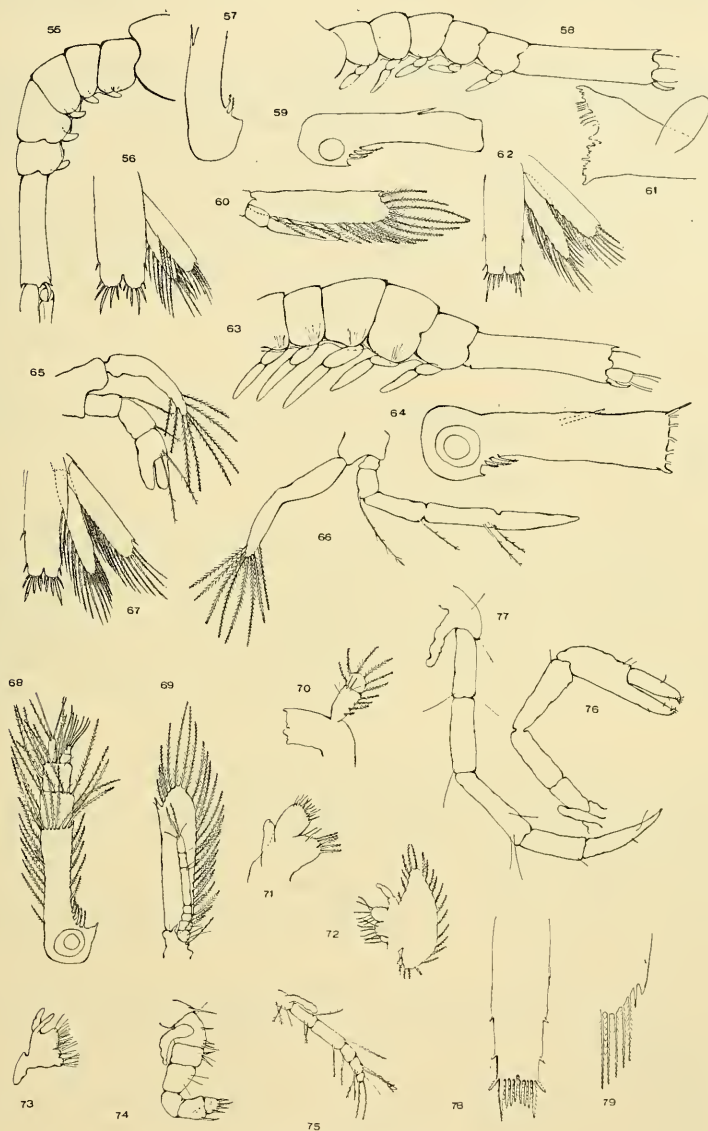
The pleopod buds have increased in size and now are clearly visible on the ventral side of the abdomen (Text-fig. 55).



*C. Third Mysis (Early Stages: Text-figs. 58-62).*

The third Mysis measures from 2.41 mm. to 2.75 mm. in length.

The carapace remains practically unchanged, and there are indications of two minute rostral teeth.



Text-figures 55-79.

55-57, Second Mysis. 55, Lateral aspect of abdomen; 56, Telson and uropods,  $\times 44$ ; 57, Basal segment of first antenna.

58-67, Third Mysis. 58, Lateral aspect of abdomen (early stage); 59, Basal segment of first antenna (early stage); 60, Second antenna,  $\times 40$ ; 61, Mandible; 62, Telson and uropods,  $\times 45$  (early stage); 63, Lateral aspect of abdomen (late stage); 64, Basal segment of first antenna (late stage); 65, First peraeopod,  $\times 98$ ; 66, Fourth peraeopod,  $\times 98$ ; 67, Telson and uropods (late stage).

68-79, First post-Mysis. 68, First antenna,  $\times 80$ ; 69, Second antenna,  $\times 44$ ; 70, Mandible,  $\times 15$ ; 71, First maxilla,  $\times 23$ ; 72, Second maxilla,  $\times 28$ ; 73, First maxillipede,  $\times 24$ ; 74, Second maxillipede,  $\times 60$ ; 75, Third maxillipede,  $\times 41$ ; 76, First peraeopod; 77, Fourth peraeopod; 78, Telson,  $\times 68$ ; 79, Distal outer corner of exopodite of uropod.

The abdominal spines remain unchanged.

The indentation between the lobes of the telson is no longer conspicuous while the same increase in the distance between the lateral telson spines continues (Text-fig. 62).

The spine on the distal outer corner of the exopodite of the uropods is becoming larger, and while the exopodite still bears twelve setae, the endopodite now bears fourteen.

The stylocerite of the first antenna (Text-fig. 59) is now very clearly formed, while the basal swelling itself now lodges the statocyst. There are three hairs on the top of the statocyst swelling and the ventral spine is still well developed. The internal branch has increased quite considerably in size, is still smaller than the fourth antennular segment, and is still unsegmented.

The number of setae on the exopodite of the second antenna (Text-fig. 60) has increased to fifteen, while the endopodite is now completely devoid of setae. The latter now consists of two segments, a long distal segment which will ultimately give rise to the typical "feeler" of the adult, and a small basal segment. A spine has appeared on the ventral aspect of the distal protopodite segment.

The mandibular palp is larger but still unsegmented and does not bear any setae (Text-fig. 61).

While the exopodite has disappeared from the first maxilla, the exopodite of the second maxilla has continued to increase in importance and now bears twelve to thirteen hairs.

The first, second and third maxillipedes have undergone no change. The endopodites of the peraeopods are now definitely longer than the exopodites and clearly four-segmented. The bifidity of the endopodites of peraeopods one, two and three, which was evident in *Mysis* I and II, has now given rise to definitely chelate appendages, while the endopodites of peraeopods four and five are long, flexible, non-chelate structures. The exopodites on all five pairs of peraeopods still carry eight terminal setae.

The pleopods (Text-fig. 58) now show a definite division into a basal portion (the protopodite) and an unsegmented distal portion (the exopodite). They are still uniramous.

#### *Late Stages of Third Mysis* (Text-figs. 63-67).

In these later stages the two rostral teeth are now quite distinct.

The indentation between the lobes of the telson (Text-fig. 67) is now very small, while the first spine is placed almost half-way up the side of the telson. The protopodite of the uropods now bears a spine.

Another spine has appeared beside the spine described previously as being present on the exopodite of the uropods. The exopodite now bears thirteen hairs, while the endopodite still bears fourteen.

There are still three hairs on the top of the statocyst swelling of the first antenna (Text-fig. 64) and the internal branch, which is slightly smaller than the fourth segment, is not segmented. The fourth segment, however, is showing signs of division into two segments.

The number of setae on the exopodite of the second antenna has increased, while the endopodite has continued to increase rapidly in size, although it is still not as long as the exopodite.

The mandibular palp is now quite large but bears no setae nor shows signs of segmentation. The cutting surface of the mandible remains unchanged.

The only change in the first maxilla is an increase in the number of setae on the proximal endite, while the exopodite of the second maxilla still bears twelve-thirteen hairs.

The first, second and third maxillipedes remain unchanged except for the acquisition of an additional seta on the distal protopodite segment of the second maxillipede at the point between articulation of the exopodite and the endopodite.

The peraeopods have undergone no important changes. The endopodites have continued to increase in importance, but the exopodites are still quite well developed and still bear the eight terminal setae (Text-figs. 65 and 66).

The pleopods (Text-fig. 63) have increased considerably in size, but are still uniramous and bear no setae.

#### POST-MYSIS STAGES.

Heldt (1938) has dealt very fully with the development of the post-Mysis stages of several Penaeid species, and has classified the post-Mysis appendage development into four different types.

As there is a gap between the first and the five much later post-Mysis stages which were taken by us in the course of this survey, it was not possible to follow in detail all changes in the post-Mysis series of stages. However, reference will be made to these trends throughout the description of the first post-Mysis stages. Since we obtained the first post-Mysis larva by moult from the last Mysis, we had no doubts about this stage.

The larva reared from Mysis III measured 2.83 mm.

The rostrum still bears only two rostral teeth.

The posterior border of the telson is now completely straight, and the indentation between the two lobes almost gone. The first and second spines are gradually moving up the lateral border of the telson (Text-fig. 78).

The small spine which appeared on the external border of the exopodite of the uropods at the previous stage, has increased in size, whilst the other exopodite spine has also increased in size and is now almost as long as a very small seta (Text-fig. 79).

There are now five hairs on the top of the statocyst swelling of the first antenna (Text-fig. 68). The internal branch is longer than the fourth antennular segment, but it is still unsegmented. The outer branch (or fourth segment) is now clearly two-segmented and there has been quite a noticeable increase in the number of hairs on all the antennular segments. The ventral spine is still present.

The exopodite of the second antenna (Text-fig. 69) bears twenty-three setae, while the endopodite is now five- to six-segmented.

The mandibular palp (Text-fig. 70) is quite a large structure, bearing six hairs on the distal segment, and four hairs on the proximal segment. The number of hairs goes on increasing, and the distal segment continues to increase in relative importance in succeeding stages. The cutting surface has now lost practically all its teeth.

In the first maxilla (Text-fig. 71) the endopodite is very much reduced, while the endites have increased considerably in size and now bear a larger number of hairs, all of which seem to be shorter and thicker than in the previous stages. The endopodite never completely disappears and at a later stage grows into a long, thin, segmented structure such as Heldt describes for her species.

The endopodite of the second maxilla (Text-fig. 72) is reduced, but grows again, and in a 9 mm. post-larval stage is just as Heldt has indicated for *Penaeus trisulcatus*. The most proximal protopodite endite has disappeared completely, while the second one remains as a very small endite bearing a very few hairs. The two most distal endites are quite well developed. The exopodite has expanded quite considerably, and is gradually forming the scaphognathite. It now bears twenty-two setae along its border.

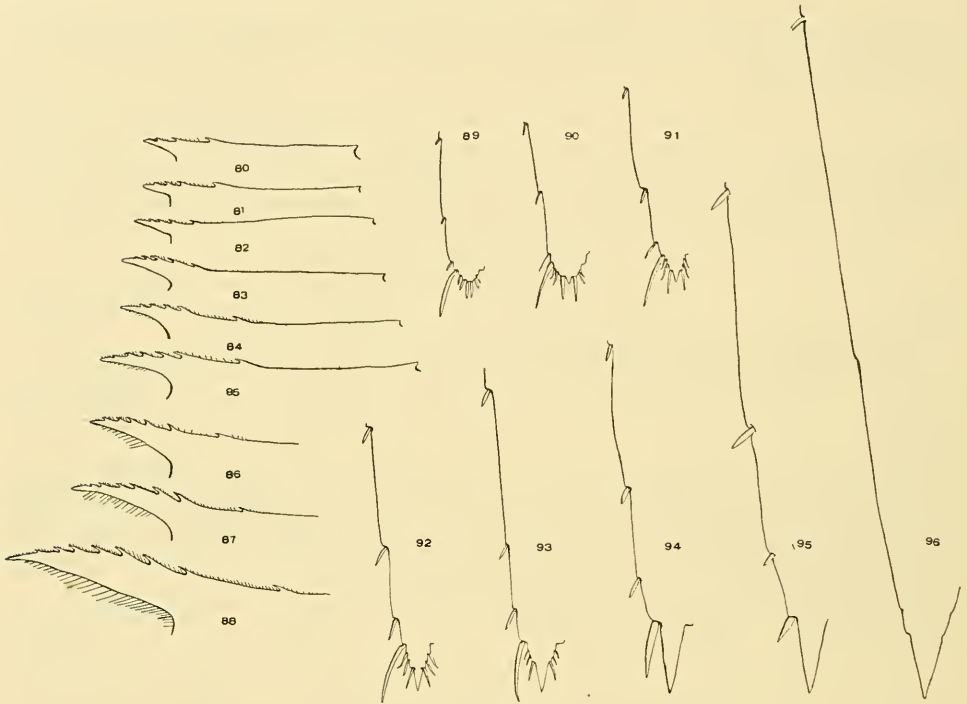
The endopodite of the first maxilliped (Text-fig. 73) has lost all signs of segmentation, while the hairs on this and the exopodite have gone also. The two protopodite segments have increased considerably in size and have acquired several more hairs on their inner borders. The endopodite, like that of the first maxilla, should regain its hairs and segments at a later stage.

The exopodites of the second (Text-fig. 74) and third (Text-fig. 75) maxillipedes remain as small withered chitinous structures, while the endopodites are quite powerful five-segmented appendages. The endopodite of maxilliped two is flexed backwards between its third and fourth segments. In the later stages the exopodites gradually develop again like the endopodites of the maxilla.



The exopodites of the five pairs of peraeopods have now almost disappeared and consist of small withered chitinous structures. They reappear at a later stage, but never develop to the extent that the exopodites of the second and third maxillipedes do.

The endopodites of the first, second and third peraeopods have developed into quite large and powerful chelate appendages, while the fourth and fifth still form rather longer, thinner, five-segmented non-chelate appendages.



Text-figures 80-96.

80-88. Rostrum. 80, 5.07 mm. stage,  $\times 52$ ; 81, 4.95 mm. stage,  $\times 52$ ; 82, 5.95 mm. stage,  $\times 52$ ; 83, 6.29 mm. stage,  $\times 52$ ; 84, 7.42 mm. stage  $\times 52$ ; 85, 7.84 mm. stage,  $\times 52$ ; 86, 9.28 mm. stage,  $\times 52$ ; 87, 11.34 mm. stage,  $\times 52$ ; 88, 16.67 mm. stage,  $\times 52$ .

89-96. Telson. 89, 5.07 mm. stage,  $\times 73$ ; 90, 4.95 mm. stage,  $\times 73$ ; 91, 6.29 mm. stage,  $\times 73$ ; 92, 7.84 mm. stage,  $\times 73$ ; 93, 9.28 mm. stage,  $\times 73$ ; 94, 11.34 mm. stage,  $\times 73$ ; 95, 16.67 mm. stage,  $\times 73$ ; 96, 23.57 mm. stage,  $\times 73$ .

The pleopods have increased in size though they are still uniramous appendages, but they now bear setae.

As Heldt (1938) has dealt very fully with the subsequent post-Mysis and post-larval development of several penaeid species, it was considered pointless to describe the further development of the individual appendages in detail, and so it was decided merely to follow the further development of the telson and see how this fitted in with the acquisition of the adult number of rostral teeth.

As mentioned above, there is quite a big gap in the post-Mysis series between the first post-Mysis and the next stage (5.07 mm.) obtained in the catches, but even so the number of rostral teeth in the latter has only increased to three (Text-fig. 80) and the posterior border of the telson is only slightly rounded. The fourth pair of telson spines have reached their greatest length at this stage (Text-fig. 89).

The faint beginnings of a fourth rostral tooth can be seen in a specimen 4.95 mm. in length (Text-fig. 81). The posterior border of the telson (Text-fig. 90) is showing signs of becoming pointed, while the fourth pair of telson spines is definitely becoming shorter. There are clearly four rostral teeth present at the 5.98 mm. stage (Text-fig. 82)

while by the time the 6.29 mm. length is reached, a trace of a fifth rostral tooth is evident (Text-fig. 83); also, the telson can be seen to have become distinctly more pointed, while the fourth pair of spines have shortened considerably (Text-fig. 91). At the 7.42 mm. stage, the fifth rostral tooth is clearly formed (Text-fig. 84).

#### POST-LARVAL STAGES.

As previously mentioned, the next stage obtained (7.84 mm.) really constitutes the first post-larval stage taken, as it is in this stage that the pleopods become biramous. A sixth rostral tooth (Text-fig. 85) is just beginning at this stage, while the posterior border of the telson has continued to lengthen and the fourth pair of spines is shorter (Text-fig. 92).

By the time the 9.28 mm. length is reached, the sixth rostral tooth is well-formed (Text-fig. 86) while the telson is showing definite signs of approaching the adult form of a long, pointed structure with no spines. The posterior border is distinctly pointed, while the fourth pair of spines only just projects beyond the pointed posterior border. The last three pairs of spines have also shortened considerably (Text-fig. 93).

At the seven rostral teeth stage (11.34 mm.) the fourth pair of spines is shorter than the pointed posterior border of the telson, and the three small spines on the telson tip have gone altogether (Text-fig. 94).

The full adult number of eight rostral teeth are present at the 16.67 mm. length (Text-fig. 88), while the remaining pairs of telson spines have shortened considerably (Text-fig. 95). By the time the 23.57 mm. length is reached, only the most proximal pair of spines (i.e., the first) remain on the telson (Text-fig. 96). This last pair of spines disappears after the next one or two moults, thus giving rise to the adult telson which bears no large lateral spines at all.

For purposes of clarity, no reference has been made to the increase in the number of setae on the dorsal surface of the telson throughout the post-Mysis and post-larval stages. There are one or two long setae present on the dorsal surface of the telson near the posterior border in the first post-Mysis stage, and these increase in number, until finally, at the 23.57 mm. stage, the telson is thickly beset with setae along its edges, on the dorsal surface—from the tip to the base. In addition, several minute spines appear on the dorsal surface, but their development is entirely separate from, and must not be confused with the gradual loss of the seven pairs of spines which were present on the telson borders right from the last Nauplius stage.

#### Acknowledgements.

The field work in connection with this study was carried out with the aid of a Commonwealth Research Grant to the late Professor W. J. Dakin.

We are very deeply indebted to Mr. and Mrs. K. H. Hargraves of Toukley, Tuggerah Lakes. Without their generosity with their boats and gear and their personal help at all hours, day and night, in all weathers, we should never have achieved any success in the field. They allowed us to turn their home into a temporary laboratory and made us always welcome.

We should also like to thank Mr. Hilton Chalmers, who took plankton catches for us periodically at the Entrance; Miss E. C. Pope, M.Sc., of the Australian Museum, for help in the field; Miss H. Newton Turner, B.Arch., Biometrician of the C.S.I.R.O. McMaster Laboratory, for checking our sampling results; Professor E. A. Briggs, D.Sc., and Mr. A. N. Colefax, B.Sc., of the Zoology Department of the University of Sydney, for reading the manuscript, and finally Professor P. D. F. Murray, D.Sc., Challis Professor of Zoology in the University of Sydney, for his advice and forbearance during the writing-up of this paper.

#### References.

- ANDERSON, W. W., KING, J. E., and LINDNER, M. J., 1949.—Early Stages in the Life History of the Common Marine Shrimp, *Penaeus setiferus* (Linn.). *Biol. Bull.*, 96, No. 2.  
 BURKENROAD, M. D., 1934.—The Penaeidea of Louisiana—with a Discussion of their World Relationships. *Bull. Amer. Mus. Nat. Hist.*, lxxviii.  
 ———, 1940.—Preliminary Description of Twenty-one New Species of Pelagic Penaeida from the Danish Oceanographical Expeditions. *Ann. Mag. Nat. Hist.*, (11) 6: 35-54.  
 ———, 1949.—Occurrence and Life Histories of Commercial Shrimps. *Science*, 110, No. 2869.

- DAKIN, W. J., 1938.—The Habits and Life History of a Penaeid Prawn (*Penaeus plebejus* Hesse). *Proc. Zool. Soc. Lond.*, 108, A, Pt. 2.
- , 1940.—Further Notes on the Life History of the King Prawn, *Penaeus plebejus* Hesse. *Rec. Aust. Mus.*, xx, No. 5.
- , 1946.—A Further Step in the Elucidation of the Strange Story of the Penaeid Prawns. *Aust. Jour. Sci.*, viii, No. 6.
- , 1946a.—Life History of a Species of *Metapenaeus* in Australian Coastal Lakes. *Nature*, 158: 99.
- GURNEY, R., 1927.—Report on the Larvae of the Crustacea Decapoda. Camb. Exped. Suez Canal. *Trans. Zool. Soc. Lond.*, xxii, Pt. 2, No. 15.
- , 1943.—The Larval Development of two Penaeid Prawns from Bermuda of the Genera *Sicyona* and *Penaeopsis*. *Proc. Zool. Soc. Lond.*, 113, B: 1-16.
- HELDT, J. H., 1938.—La Reproduction chez les Crustacés Décapodes de la Famille des Pénéides. *Ann. Inst. Oceanog. Monaco*, xviii, 2: 31-206.
- IDYLL, C. P., 1950.—The Commercial Shrimp Industry of Florida. *Florida Board of Conservation*, Educ. Ser. No. 6.
- PANIKKAR, N. K., and AIYAR, R. G., 1939.—Observations on Breeding in Brackish-water Animals of Madras. *Proc. Ind. Acad. Sci.*, ix, No. 6, Sec. B: 343-364.
- PEARSON, J. C., 1939.—The Early Life Histories of Some American Penaeidae, chiefly the Commercial Shrimp, *Penaeus setiferus* (Linn.). *U.S. Dept. Commerce, Bur. of Fisheries*, Bull. 30.

## EXPLANATION OF PLATE XII.

Fig. 1.—Head of a mature female "Greasy Back" showing rostrum.

Fig. 2.—Adult female dissected to show gonads.

Fig. 3.—Eggs with Nauplii showing through egg membrane and one hatched nauplius.

(Photos. Gwen Burns.)